Beauty: In the gonads of the beholder — and the beheld

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I remember being puzzled as a teenager by some of the male sex symbols whose posters adorned girls' dorm rooms. Robert Redford and Paul Newman I could understand, but Humphrey Bogart, with his weak chin and crooked smile? Or French heart-throb Jean-Paul Belmondo, with his big mouth and prodigious Gallic nose? Why would a girl want to dote on what seemed to me quite unattractive faces? It is not just the face, of course, that is the attraction in these cases, but the voice, the character, the swagger – the whole package. Still, it was the face that was there, staring back from the walls.

We react strongly to faces, and we read a lot into them. Specialized sets of neurons seem to be set aside for recognizing small differences in facial features as the bases of individual recognition (Calder and Nummenmaa, 2007; Gobbini and Haxby, 2006; Ng et al., 2006; Sereno and Huang, 2006). We read emotion from faces with remarkable sensitivity, often relaying that emotion through our own mirror-neuron circuits (Calder and Nummenmaa, 2007; Moody et al., 2007; Schulte-Ruther et al., 2007). And we react emotionally to faces in complex ways, with greater or lesser degrees of trust, apprehension, defiance, and of course, sexual attraction.

But what features make an attractive face? Do people agree on those features? And why should those particular features be attractive? There is actually considerable convergence of opinion among behavioral scientists of different stripes on some aspects

of these questions. For one thing, infants as young as 2 to 3 months old show a preference for the same faces that adults rate as more attractive, suggesting that criteria of attractiveness are available without the need for much in the way of learning or social conditioning (Langlois et al., 1987). For another, there is remarkable cross-cultural consistency in ratings of facial attractiveness, even when people are rating faces from populations they have never encountered (Jones et al. 1995).

What the criteria of facial attractiveness are, however, is in greater dispute. In 1990, Langlois and Roggman reported on a new method for "blending" facial images on a computer to produce composites that averaged the features of the individual faces they were generated from (Langlois and Roggman, 1990). They found remarkable consistency among subjects in rating composite faces as more attractive than individual faces. The higher the number of faces blended, the more attractive the resulting "average" face. Langlois and her colleagues further demonstrated that these "average" faces were also preferred by infants and by people of different genetic and cultural background (Langlois et al., 1994). They even suggested as an evolutionary consequence that the preference for average faces serves to prevent Fisherian "runaway selection" for particular facial traits. Francis Galton actually made similar observations in the 19th century based on superimposing photographs, suggesting that average faces obscured the telltale signs of criminality and depravity that might be apparent in individuals (Galton, 1878).

More research soon followed, using computer-manipulated faces to explore the basis of attractiveness and coming up with somewhat different answers. Jones presented evidence that more neotenous, or "youthful," facial features than average are considered more attractive (Jones, 1995), while Perrett et al. found a preference for more "feminized" faces than average (Perrett et al., 1998). In both of these cases the preferences were consistent for both male and female subjects rating both male and female faces, whether of same or different genetic and cultural background.

But in a follow-up to the Perrett et al. study, the same group reported a new twist (Penton-Voak et al., 1999). Female ratings of male facial attractiveness vary with the raters' menstrual cycle. Although the general preference for somewhat feminized faces was confirmed in this study, women judged to be in the middle of their menstrual cycles showed a shift in preference toward less feminized faces. This tendency was particularly striking when women were asked to rate attractiveness for a partner in a "short-term sexual relationship" versus a "long-term relationship." The faces used in these studies were "feminized" or "masculinized" on the computer by differential blending of actual male and female faces. But the authors, in interpreting their findings, suggested that in real male faces a similar "feminine-masculine" axis of variation represents a cue to male testosterone levels. A shift in female preference toward higher testosterone men at midcycle and for short-term mating might, they reasoned, be a means for choosing "good genes." But to make this argument they had to invoke the often challenging logic of the "handicap principle": high testosterone by itself suppresses immune function (a bad thing); therefore men who flourish despite this handicap must have "good traits" that

more than compensate (a good thing). By choosing a manifestly "bad thing," females are actually choosing a non-manifest "good thing." (If this logic seems a bit dicey to you, as it often does to me, there is a large literature to wallow in.)

By this point, however, the logical scaffolding supporting an adaptive understanding of judgments of facial attractiveness seems to be getting a little top-heavy with assumptions. A computer-generated facial "trait" (relative femininity-masculinity) may or may not correspond to a trait in "real" faces. Female preference for this trait may or may not depend on a woman's actual, rather than inferred, hormonal levels. If the computer-generated facial trait exists in "real" male faces, it may or may not be correlated with actual testosterone levels. And if it correlates with testosterone levels, those levels may or may not be correlated with other male traits that would confer fitness advantage on a woman's offspring. As the assumptions proliferate, one has to worry about objectivity. Are we trying too hard to see in the data what we want to find?

In this issue of *Hormones and Behavior*, Roney and Simmons present a study that goes a long way toward reducing the number of assumptions in play. Rather than relying on computer-generated faces, they assess women's ratings of the attractiveness of real male faces. Rather than assume that the characteristics of these faces are cues to testosterone levels, they measure the testosterone levels of their male subjects. Rather than infer the hormonal status of their female raters from menstrual dates, they measure their estrogen levels. The results demonstrate than the degree of female preference for the faces of men with higher actual testosterone levels is positively correlated with actual

female estrogen levels, tracking those levels across the menstrual cycle. Beneath face-to-face attraction they discover gonad-to-gonad resonance!

But as is always true in science, progress toward resolving one part of a puzzle often helps to bring another part of the puzzle into clearer focus. If women's preference for men's faces is really a reproductive state dependent preference for male testosterone levels, what function does this serve? Roney and Simmons seem content to rely on a "handicap principle" interpretation of this facultative preference. But I suggest that this part of the puzzle now deserves more scrutiny.

One issue that merits attention concerns the interpretation of the preference for high testosterone men as a preference for a stable male trait as opposed to a variable male state. Men's testosterone levels change dramatically, not on a regular monthly cycle like female estradiol levels, but in many predictable ways. Roney and Simmons commendably try to control for circadian variation in their measurements of testosterone, but there are numerous other sources of within-individual variance in testosterone, both short and long term, including mating and parenting status (Gray et al., 2002), exposure to other males and females (Roney et al., 2007), exercise or physical exertion (Di Luigi et al., 2006), age (Ellison et al., 2002), and maturational status (Di Luigi et al., 2006). The last two on this list perhaps deserve special attention. It is notable that virtually all of the recent studies of facial attractiveness have been conducted with university student populations, both as sources of the faces and as raters (Rhodes, 2006). Particularly in this age group male testosterone levels may be strongly affected by a wide range of

maturational status. Could the estrogen-dependent female preference for higher testosterone men be a preference for more mature late-adolescent men? Such a possibility would suggest that women, at least in a similar age group, are not choosing stable male traits, but current male attributes. This would in turn challenge the "handicap principle" interpretation of the functional significance to the preference.

Advocates of the trait preference interpretation might argue that, theoretically, we expect female choice to shift toward traits rather than states as the context of choice becomes more narrowly limited to short-term mating. But we should always be prepared to have our theoretical expectations challenged by data. One approach to testing the validity of preference for high testosterone as preference for a trait would be to move to a broader age range of both women and men. If male faces are cues to male testosterone state, then female preferences at mid-cycle should converge on young adult male faces, an age when absolute male testosterone is at its peak, as are presumably other transient male states such as competitive ability and sexual virility. If, on the other hand, female mid-cycle preferences are truly for stable male traits, then age-corrected testosterone should emerge as the best predictor of female choice.

Another question to pursue is the stability of the female preference with changing female state. We have already established that preference varies across the menstrual cycle as a function of female hormonal status. But this has only been clearly demonstrated in one particular age group who may share certain aspects of underlying reproductive strategy as a function of age and parity. Would older, higher parity women

show the same preference bias, or to the same degree? Roney and Simmons already invoke in their discussion the necessity of thinking about variation in female fecundity in a natural environment as a context for any functional interpretation. That context not only includes long periods of infecundity due to lactation, but variation in fecundity with age and energetics. In addition, life history theory predicts changes in reproductive effort with age and parity. Once we conceive of perceptions of attractiveness as reflections of facultative reproductive strategies, the dimensions of facultative variation proliferate. Again, broadening the range of female reproductive states sampled to include lactating and pregnant women, women of different ages and parities, and women in different energetic conditions, might be illuminating.

In the end we may be left with the "Bogart and Belmondo problem." The world comes into our consciousness as a gestalt, synthesized in our brains from a host of different sensory and cognitive inputs. Averageness, youthfulness, masculinity-femininity, current states and stable traits may all play a role in our perceptions of attractiveness. Roney and Simmons have helped to establish more firmly the fact that our concepts of physical beauty are rooted in our biology, shaped by natural selection, and not merely acquired tastes determined by culture and advertising, as powerful as those influences may be. But although we can be fairly sure our gonads are speaking to us in our judgments of attractiveness, we can't yet be sure what they are saying.

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